COEVOLUTION OF *FICUS* AND AGAONIDAE

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There are many kinds of wasps, representing several families which develop in the syconia of *Ficus*; however only species of the family Agaonidae act as pollinators. The other fig wasps are parasites either of the syconia or of the Agaonidae. Most of these parasites are unable to penetrate the syconia; they usually have very long ovipositors which allow them to pierce the fig wall and oviposit inside the fig.

Because the agaonids develop and spend most of their lives inside the figs, they responded more to the morphology of the syconial entrance (the ostiolum) and to the distribution, physiology, and morphology of the flowers than to the gross morphological changes suffered by other parts of the fig tree. The modifications found in the syconia and in the flowers of the different groups of figs as well as those found in the bodies of their symbiotic agaonids seem to be the result of mutual adaptations which favored their symbiotic association.

The female agaonid is winged and has structures which help her to carry pollen, to enter the fig through the ostiolum, and to oviposit in the female flowers inside the syconium. The males on the contrary are apterous and usually do not leave the fig in which they develop.

The syconium is a completely closed inflorescence with the flowers located in the internal wall (Figs. 3–4). The only access to the interior of the fig is a very complicated entrance called the ostiolum, which is covered with bracts (Figs. 1–2). There are three kinds of flowers in the fig: long-styled or true female flowers, which usually set seeds; gall flowers, which are short-styled female flowers where the wasps oviposit, and male flowers (Figs. 3–4).

The fig inflorescence is characterized by its high degree of protogyny, the male flowers maturing several weeks after the female. Another characteristic of *Ficus* is the high degree of synchronization in the development of the syconia; all the figs in a tree are pollinated at the same time and thereafter ripen together.

The developmental period of the syconium is divided into several phases (Galil & Eisikowitch, 1968): prefloral phase, which lasts from the time of appearance of the syconial buds to the maturation of the female flowers; the female phase, lasting no more than three days, which corresponds to that time when the female flowers are receptive for pollination and oviposition, during this period the ostiolar scales become loose to facilitate the entrance of the female agaonids; the interfloral phase, which lasts from the end of the pollination and oviposition phase to the maturation of male flowers and the eclosion of a new generation of wasps from the galls. The interfloral phase is usually very constant for each species of fig and seems to be determined by the developing agaonids inside the figs. This phase I have found to last from 15 to 100 days for different neotropical figs (Table 1). The male phase corresponds to the time when the male flowers

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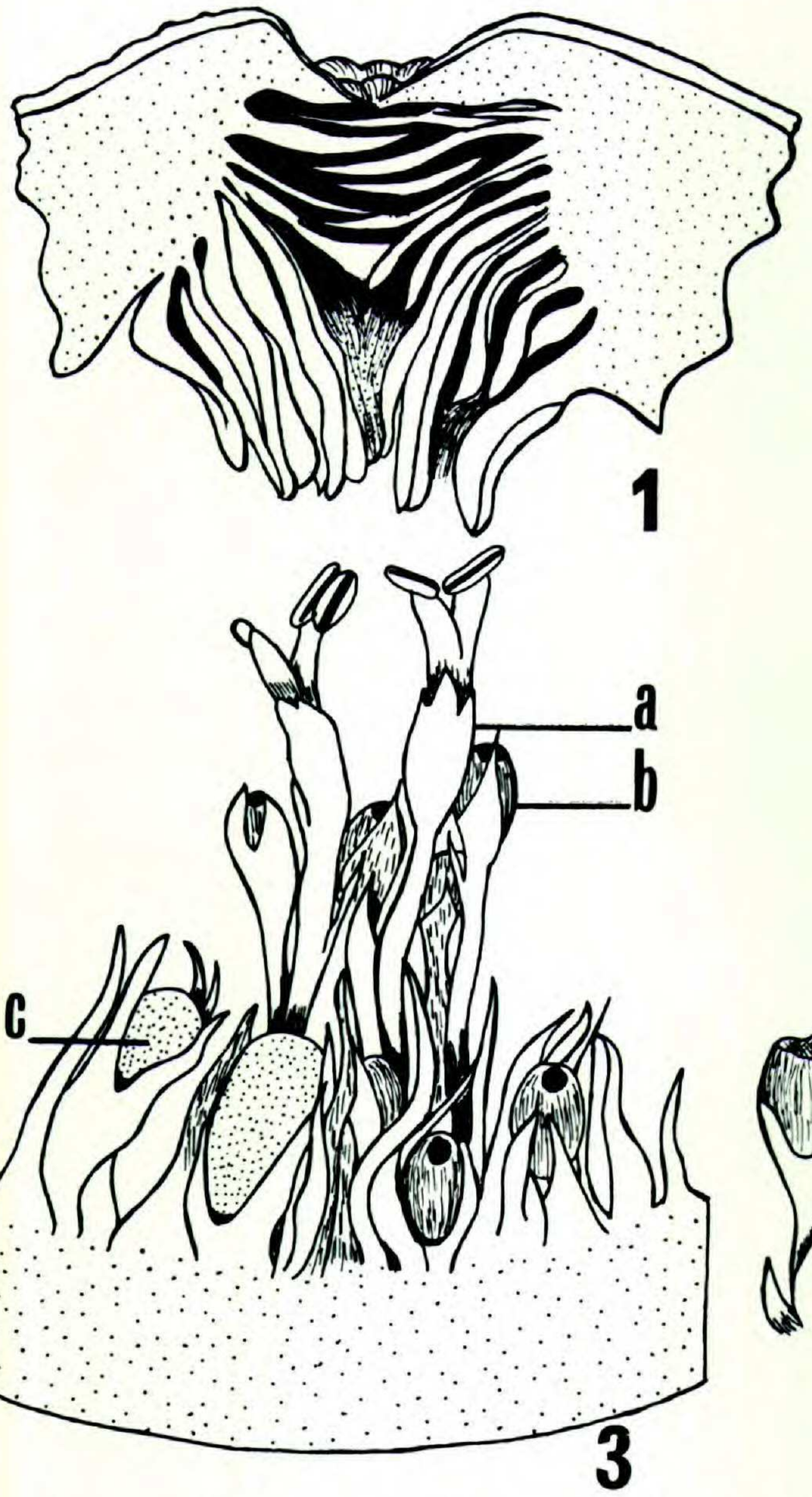
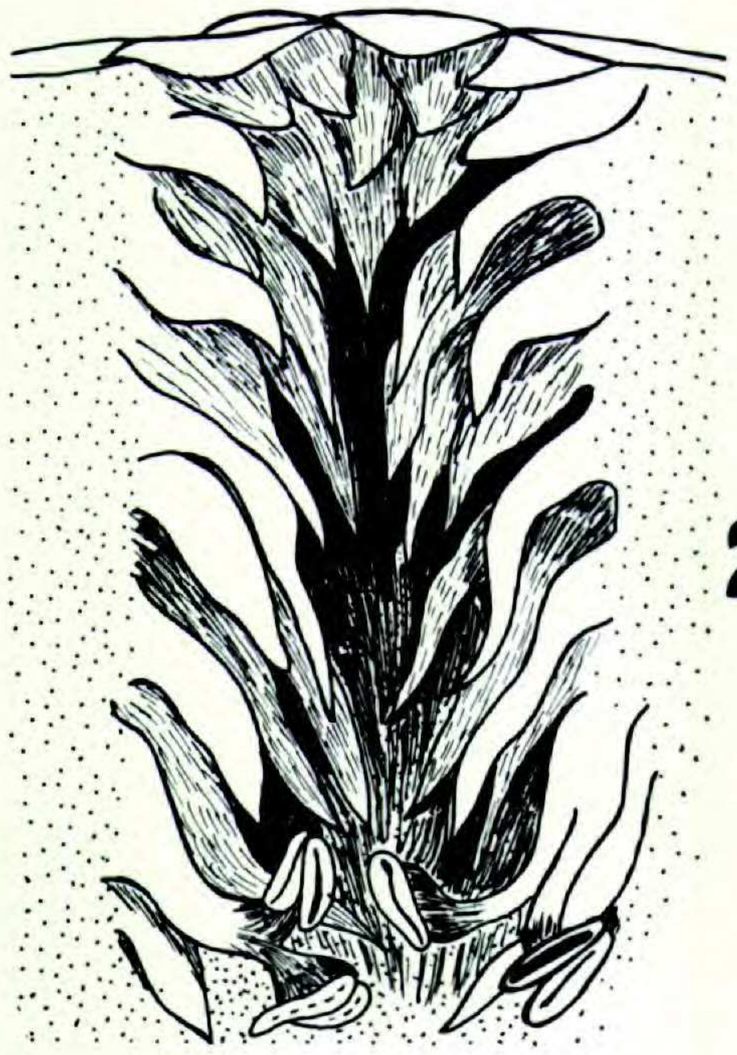
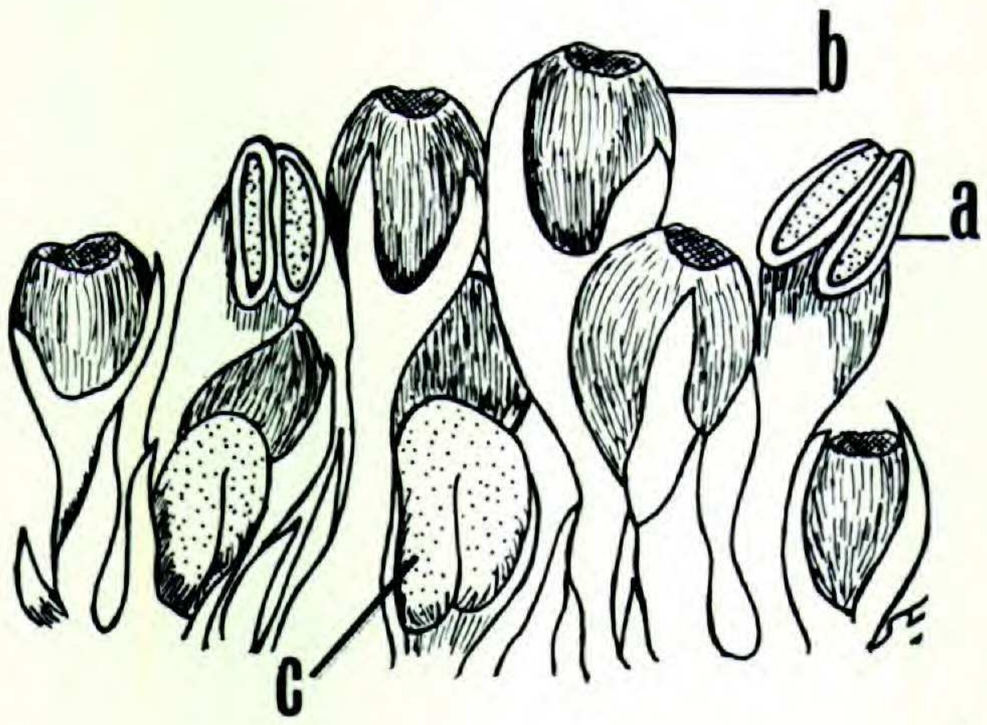






FIGURES 1–4. Longitudinal section through the ostiola and the interior of four syconia at male phase.—1. Ostiolum of the Old World *Ficus carica* (after Grandi, 1920).—2. Ostiolum of the New World *Ficus maxima*.—3. Section through the interior of the syconium of *F. maxima* (a, male flower; b, gall flower, and c, mature seed).—4. Section through interior of a New World *Urostigma* fig (section *Americana*); a, male flower; b, gall flower, and c, mature seed.

mature. At this phase the female wasps eclose from their galls after copulation has occurred, search for the ripe anthers, and escape from the figs carrying pollen which they will take to other figs in the female phase.

The male phase lasts only a few hours and usually occurs during early morning in the Neotropics. Once the female agaonids and other fig wasps escape from the mature figs, the syconia become completely ripe, that is, soft and juicy, and the post-floral phase starts. In this phase the figs become edible for frugivorous vertebrates.

Thus, the syconia are traps entered by the female agaonids, which pollinate, oviposit and die inside the syconial cavity. The female wasps which escape from the male phase figs belong to the new generation; the apterous males usually

TABLE 1. Length of interfloral phases of different Neotropical species of *Ficus*. DeWolf (1960) considers that *F. insipida*,* *F. glabrata*,* and *F. crassiuscula** are one species (*F. insipida* Willd.); he also considers that *F. turbinata*** and *F. hensleyana*** are one species (*F. citrifolia* P. Mill.), and that *F. involuta**** and *F. obtusifolia**** are one species (*F. obtusifolia* H.B.K.).

Ficus	Number of days
*F. insipida**	15
F. nymphaeaefolia	20
F. myriacycea	23–28
F. trigonata	27
*F. turbinata***	28
F. maxima	27–30
*F. glabrata**	30
*F. hemsleyana***	27–30
F. oerstediana (= *F. perforata*)	30
F. tonduzii	31
F. bullenei	37
Ficus sp. (No. 4 of Venezuela) (Ramirez, 1970)	41–43
F. popenoi	43
*F. involuta****	43
*F. obtusifolia****	44–45
*F. crassiuscula**	50
F. lapathifolia	56
F. paraensis	60
F. torresiana	70
F. padifolia	100

die inside the fig after mating and gnawing an exit for the escape of their female siblings.

ASSOCIATION OF DIFFERENT SYCONIAL CHARACTERS WITH SOME MORPHOLOGICAL AND BIOLOGICAL CHARACTERS

The *Ficus*-pollinating agaonid species have become completely adapted in their morphology and physiology to the species of fig in which they develop, while the syconial features of each *Ficus* species also exhibit a morphological and physiological adjustment to the corresponding pollinator species. The most striking cases of coevolution between *Ficus* and Agaonidae are explained below.

MONOECISM

This condition is found in those figs in which the true "female flowers," "gall flowers," and male flowers develop in the same syconium; thus the production of pollen, seeds, and wasps occurs in the same syconium (Figs. 3–4). The monoecious figs have two kinds of female flowers which differ mainly in the length of the styles and size of the stalks. The stalked flowers usually have short styles which are as long as or shorter than the length of the ovipositor of the symbiotic agaonid of the fig. The short-styled flowers are used for oviposition; however, these kinds of flowers may also function as true female flowers which are transformed into seeds if they are pollinated artificially or by the agaonid. The other

kind of female flowers have styles which are usually much longer than the ovipositor of the agaonid; thus, the wasps are unable to oviposit in their ovaries. The long-styled female flowers usually become transformed into seeds if pollinated by the egg-laying wasps.

Monoecious figs: Subgenus *Urostigma*, subgenus *Pharmacosycea*, section *Sycomorus* (*sensu* Ramírez, 1974), and two species of section *Sycocarpus* (*F. microdictya* and *F. pritchardii*).

Associated characters of the agaonids: Presence of long ovipositors which are usually as long as or longer than the gasters. Such long ovipositors are necessary because the styles of gall flowers of monoecious figs are longer than those of dioecious figs.

Agaonids with long ovipositors: *Agaon*, *Alfonsiella*, *Allotriozoon*, *Blastophaga* groups E, F, G, the *Ceratosolen* which inhabit section *Sycomorus* (*sensu* Ramírez, 1974), and two species of section *Sycocarpus*, the megarhophalus group, *Dolichoris*, *Elisabethiella*, *Eupristina*, *Maniella*, *Paragaon*, *Pegoscapus*, *Pleistodontes*, *Tetrapus*, and *Waterstoniella*.

DIOECISM

This condition exists in those figs in which the long-styled female flowers (true "female flowers") are located in one kind of syconium the "seed fig," while the short-styled female flowers, the "gall flowers," and the male flowers grow in another kind of syconium, the "gall fig." The seed fig usually has no functional male flowers. The two kinds of syconia ("gall" and seed "figs") usually occur in the same tree but in some species (*e.g. F. carica*, the edible fig) the gall and seed figs are located in different trees. Both kinds of figs attract the egg-laying agaonids and are entered by them. The long-styled female flowers of the seed fig are pollinated by the agaonids, and as rule most, if not all, become seeds because the wasps are unable to oviposit in their ovaries. In the gall fig, the agaonids are able to oviposit in the majority, if not all, the female flowers which therefore become transformed into psenocarps or galls. It is not known for sure if the gall flowers are receptive when they are artificially pollinated; although some seeds have been occasionally found in the gall figs of *F. carica*. The "gall figs" and "seed figs" are quite similar externally and are confused by the agaonids, although they show some differences, *e.g.* the gall figs are usually smaller, less colorful, less sweet and much drier at male phase than the seed figs. Gall figs are usually characterized by the presence of abundant sclerotic cells on the receptacular wall, and they become ripe much faster than the seed figs pollinated at the same time. It seems probable that the precocious maturity of the gall figs is due to the presence of the developing agaonids. Corner (1933) reports for *F. fistulosa* and *F. variegata* that the gall receptacles develop and ripen in two-thirds of the time required by the female receptacles which persist full-sized on the plant for a month or so longer.

Group of dioecious figs: Subgenus *Ficus* and subgenus *Sycomorus* (both *sensu* Ramírez, 1974) except section *Sycomorus* and two species of the section *Sycocarpus* which are monoecious.

Associated character of the agaonids: Presence of very short slightly projecting ovipositors, related to the short styles of gall flowers of all dioecious figs.

Agaonids with short ovipositors: *Blastophaga* groups A, B, C, and D and most *Ceratosolen*, except the pollinators of section *Sycomorus* (*sensu* Ramírez, 1974) and of *F. microdictya* and *F. pritchardii* of section *Sycocarpus*.

ENTRANCE OF POLLINATORS THROUGH OSTIOLE

A. *Syconial entrance with superficial interleafing bracts*: This type of entrance (as in Fig. 1) is found in most *Ficus* with the exception of section *Pharmacosycea* of subgenus *Pharmacosycea* (Fig. 2).

Associated characters of the agaonids: Breakage of the antennae and wings when the wasps enter the figs at female phase. The breakage of the structures mentioned probably facilitates the entrance into the figs; certainly the wasps tolerate this breakage as they enter among the tightly fitting bracts.

Wasps which break the antennae and wings: All agaonidae except those of genus *Tetrapus*. *Sycophaga sycomori* (Sycophaginae), a torymid that enters the fig, also breaks the antennae and wings when it passes through the interleafing superficial scales of its host *Ficus sycomorus*.

B. *Syconial entrance without superficial interleafing bracts*: This condition occurs only in New World section *Pharmacosycea* (Fig. 2) which is exclusively pollinated by *Tetrapus*.

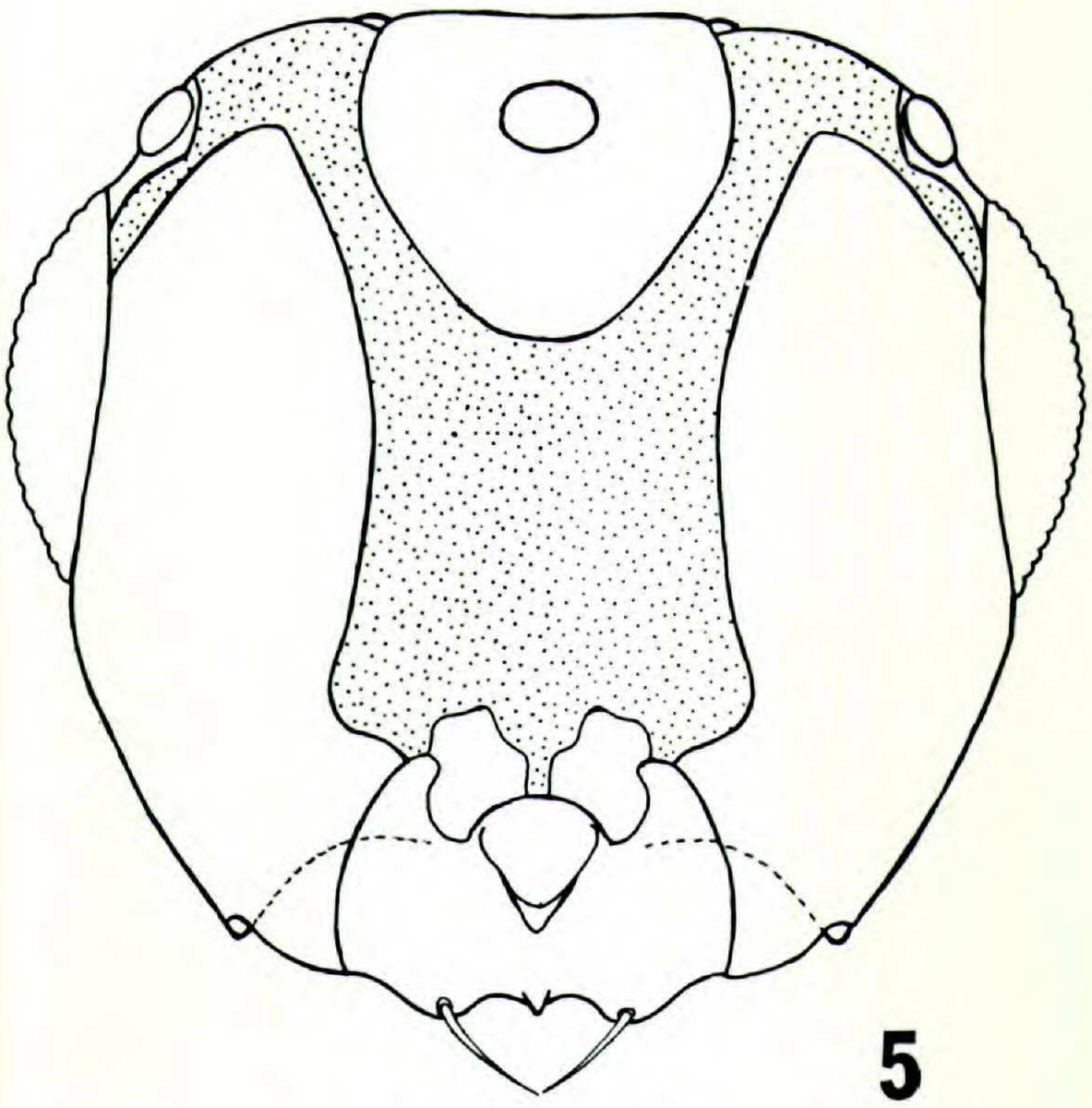
Associated characters of Tetrapus: They break neither the antennae nor the wings when they enter the figs at female phase.

C. *Syconial entrance with helicoidal bract arrangement*: The bracts of this type of ostiolum (Fig. 1) are imbricated and located in such way that they form a helicoidal entrance. The agaonids that penetrate figs with that type of ostiola have to turn around several times among the ostiolar bracts to reach the internal cavity of the syconium.

Groups of figs with helicoidal ostiolar entrance: Subgenera *Ficus* and *Sycomorus* (*sensu* Ramírez, 1974) and the sections *Americana, Conosycea, Leucogyne, Stilpphyllum*, and *Urostigma*.

Associated characters of the agaonids. A) Subquadrangular or subhemispherical flattened heads which are usually as long as broad across the eyes (as in Fig. 5); B) short mandibular appendages with lamellae (as in Fig. 6); short subhemispherical or subtriangular depressed scapes; D) usually long scale-like antennal processes (as in Fig. 9).

Groups of agaonids with the characters described: *Blastophaga* (subgenera, *Blastophaga, Eupristina, Parapristina, Pegoscapus*, and *Waterstoniella*), *Ceratosolen*, and *Liporrhopalum*. All the characters described above for the head characterize the megarrhopalus group and *Dolichoris vasculosae*, but their antennal processes are short and not scale like. *Dolichoris* is peculiar in having unidentate mandibular lamellae. *Sycophaga sycomori* (Sycophaginae) and the wasps of the tribe Sycoecini except *Seres armipes* have subquadrangular flattened heads and also enter figs with helicoidal ostiolar entrances.



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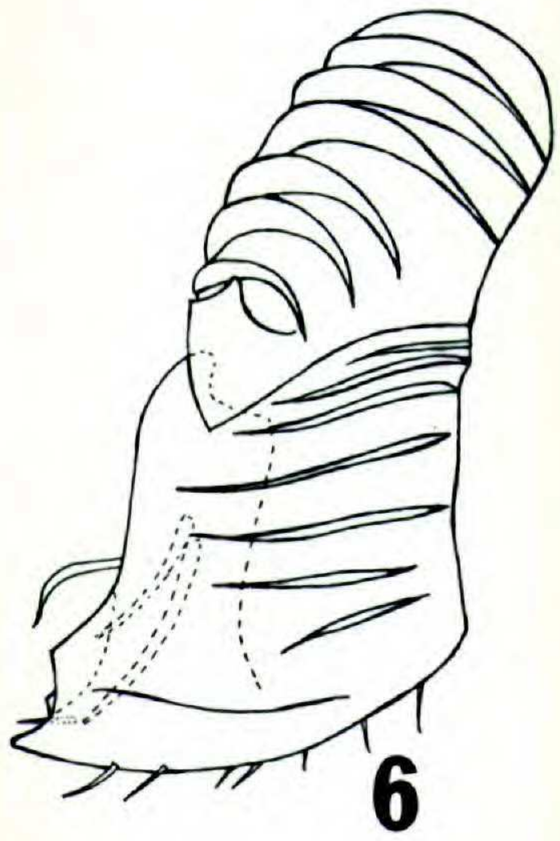

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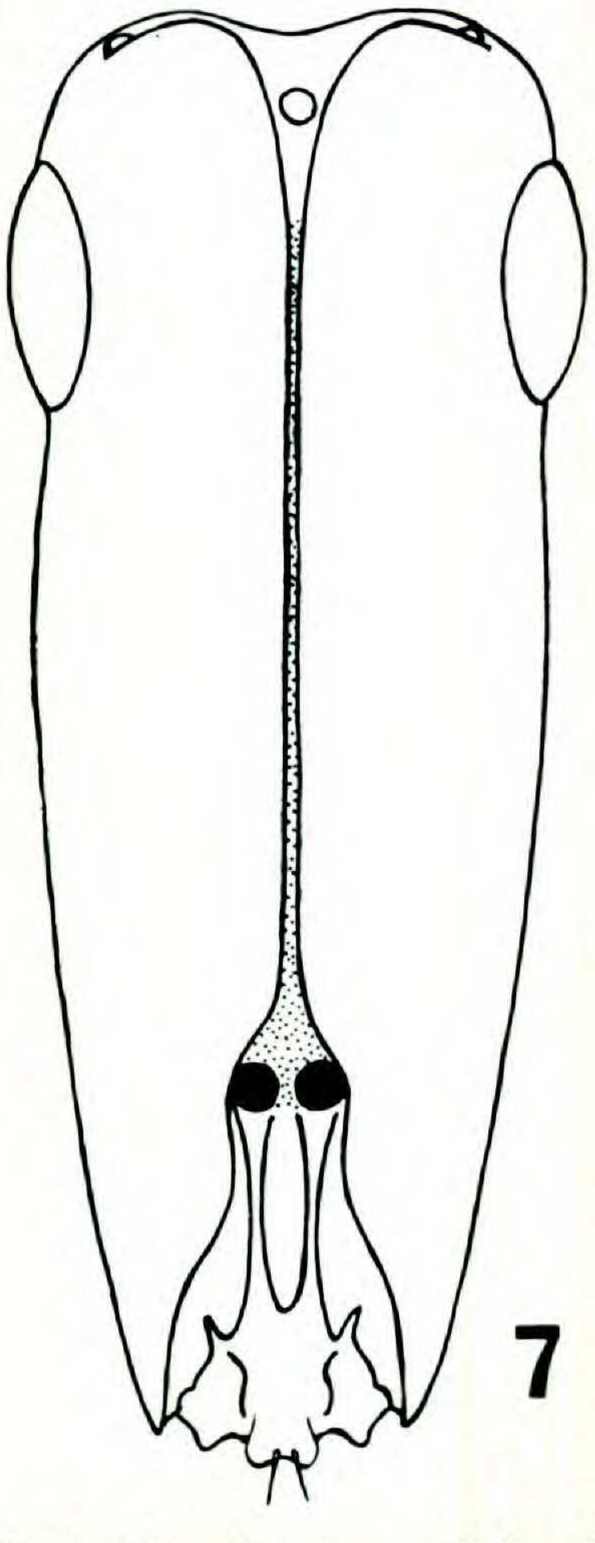

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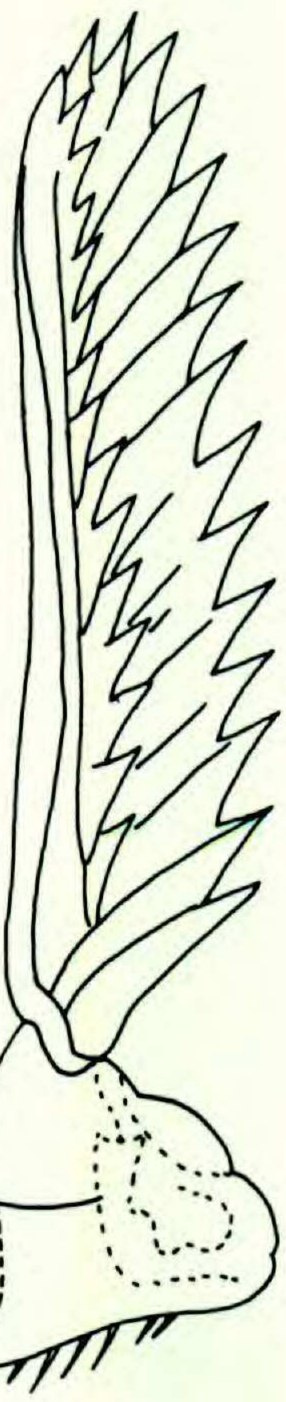

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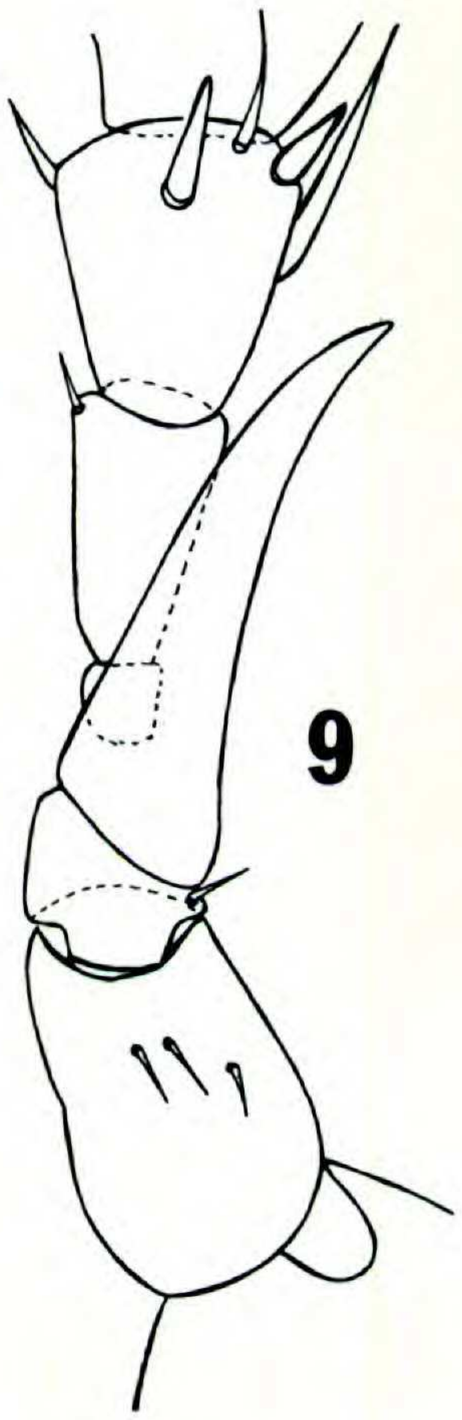

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FIGURES 5–9. Dorsal views of heads, mandibles and antennal process.—5. Head of *Maniella delhiensis*, the pollinator of *F. tsiella*, (section *Leucogyne*), a fig with helicoidal ostiolar entrance (as in Fig. 1).—6. Mandible of *Blastophaga amabilis*, the pollinator of *F. nymphaeaefolia* (section *Americana*), a fig with helicoidal ostiolar entrance.—7. Head of *Pleistodontes regalis* (after Grandi, 1952, Fig. IX, 1), the pollinator of *F. pleurocarpa* (section *Malvanthera*), a fig with tubular ostiolar entrance as in Fig. 2.—8. Mandible of *Tetrapus costaricanus*, the pollinator of *F. glabrata* (section *Pharmacosycea*), a fig with tubular ostiolar entrance.—9. Base of antennal flagellum of *Maniella delhiensis* showing the antennal scale-like process.

D. *Syconial tubular entrance*: This kind of ostiolum has the majority of the bracts pointing down, that is inflexed (as in Fig. 2) so that they form a long tubular ostiolar tunnel through which the wasps enter. Sections *Galoglychia* and *Malvanthera* have 2 or 3 interleafing superficial ostiolar bracts on top of the tubular tunnel. The wasps penetrate in a straight way, although they break the antennae and wings under the superficial bracts.

Groups of figs with tubular ostiolar tunnel: Sections *Galoglychia* and *Malvanthera* of subgenus *Urostigma* and section *Pharmacosycea* (Fig. 2) of subgenus *Pharmacosycea*.

Associated characters of the agaonids: Head usually long, in some agaonids more than one-half as long as broad across the eyes (Fig. 7); scapes long; antennal processes short, not scale-like, unsegmented; mandibular appendages long, usually with transverse rows of teeth (Fig. 8). The type of ostiolum mentioned seems also to be associated with the presence of odontoid spiniform processes on the front tarsi in *Pleistodontes* and *Tetrapus*. *Seres armipes* (subfamily Sycophaginae, tribe Sycoecini), a wasp that also penetrates a fig with long tubular ostiolar entrance, also has a long head and spiny processes on the front tibiae.

Groups of agaonids with the characters described: *Alfonsiella*, *Agaon*, *Allotriozoon*, *Elisabethiella*, *Paragaon*, *Pleistodontes*, and *Tetrapus*.

ESCAPE OF FIG WASPS FROM SYCONIA

A. *Dehiscence of the gall-fig at male phase*: This condition exists in the moraceous genus *Sparattosyce* in which the male inflorescences splits when ripe, thus exposing the male flowers to the wind that diseminates the pollen; the female inflorescences also splits when ripe. The dehiscence of the gall figs is a condition that permits the agaonids to escape at male phase.

Related characters of the agaonids: The males do not gnaw exits for the escape of the females from the figs at male phase.

Group of agaonids with the character described: The agaonids inhabiting section *Ficus* subseries *Dehiscentes* of Corner (1965), that is, those of *Blastophaga* group A.

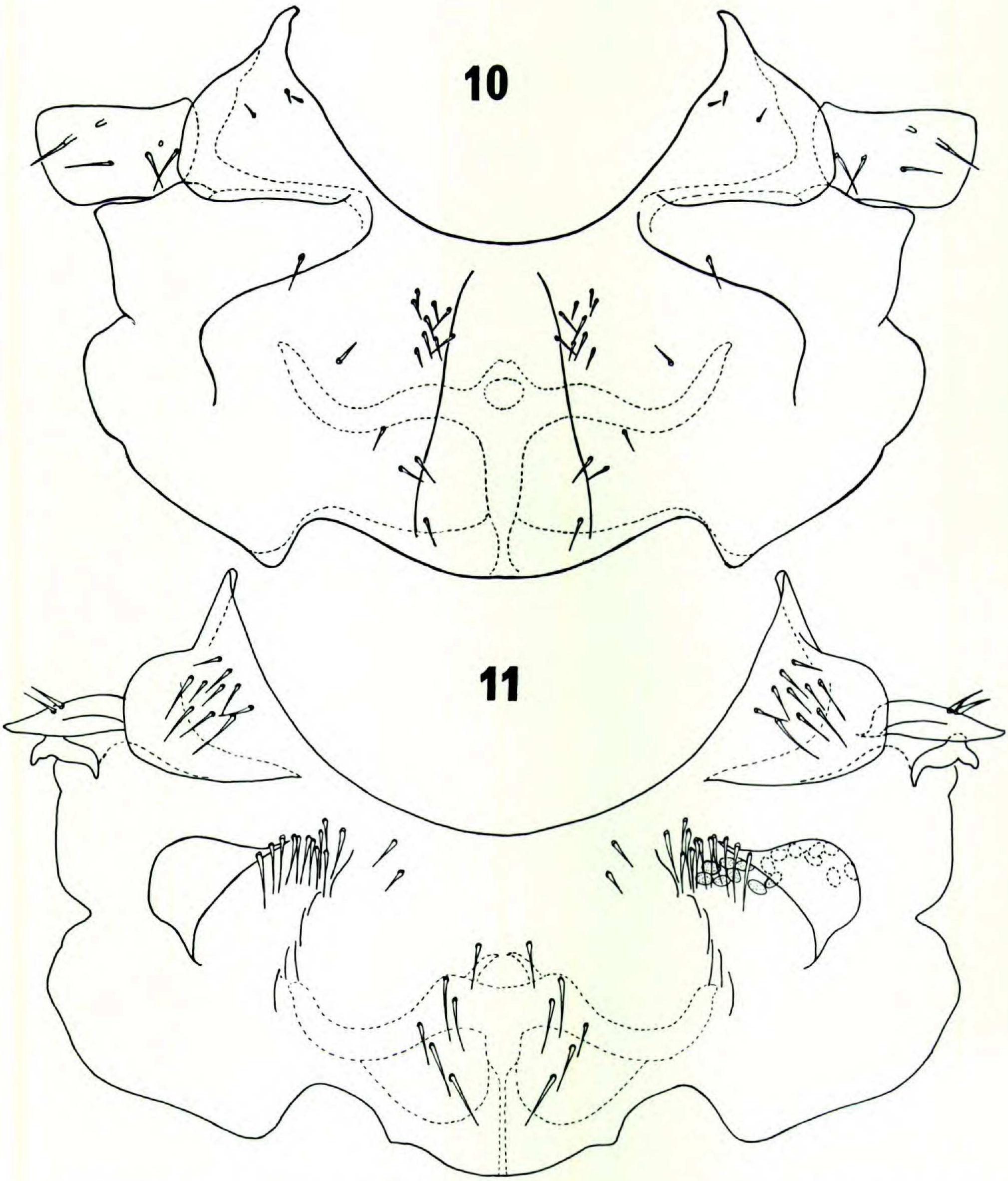
B. *Natural opening of the ostiolum at male phase*: In some groups of fig the ostiolar bracts become loose and form a natural exit for the escape of the agaonids as well as other sycophillous wasps.

Groups of figs with ostiola which open naturally at male phase: Sections *Ficus*, *Eriosycea* (both *sensu* Ramírez, 1974), *Kalosyce*, *Rhizocladus*, and probably *Sinosycidium*. It is not known if the figs of section *Paleomorphe* open the ostiola naturally.

Associated characters of the agaonids: The males do not gnaw exits for the escape of the females at male phase.

Groups of wasps with the character described: *Blastophaga* groups A and B, also probably *Liporrhopalum*.

C. *Ostiola which do not open at male phase*: In the majority of figs the ostiolar bracts do not open when the fig reaches maturity.



FIGURES 10–11. Mesosterna of *Blastophaga* wasps.—10. *Blastophaga psenes* (of *Blastophaga* group A), the pollinator of *Ficus carica* (section *Ficus*), a fig with abundant male flowers as in Fig. 3. Note the absence of corbiculae.—11. *Blastophaga malavarensis* the pollinator of *F. virens* (section *Urostigma*), a fig with male flowers as in Fig. 4. Note some grains of pollen in the right corbicula.

Groups of figs whose ostiola do not open naturally: Subgenera *Urostigma*, *Pharmacosycea*, *Sycomorus* (*sensu* Ramírez, 1974), and sections *Phaeopilosae* and *Sycidium* of subgenus *Ficus* (*sensu* Ramírez, 1974).

Associated characters of the agaonids: The males gnaw exits through the receptacular wall for the escape of the females. In most figs the males pierce the exit through the ostiolum.

Groups of agaonids which gnaw exits for the escape of the females: All the pollinators which inhabit the subgenera *Urostigma*, *Pharmacosycea*, and *Sycomorus* and the sections *Phaeopilosae* and *Sycidium* of *Ficus*.

MALE FLOWERS

Several characteristics of the figs' male flowers are associated with the amount of pollen produced and with the system of pollen transport used by the agaonids. The presence of numerous male flowers (about 35 or more per 100 gall flowers) and of long-stalked male flowers with large anthers from which the pollen comes out naturally is associated with the production of abundant pollen.

Groups of figs with the characteristics mentioned: Sections *Ficus*, *Kalosyce*, *Rhizocladus*, and probably *Sinosycidium* of subgenus *Ficus* (*sensu* Ramírez, 1974); section *Pharmacosycea* of the subgenus *Pharmacosycea* (Fig. 3); section *Malvanthera* and probably the series *Glaberrimae*, some subseries of series *Drupaceae*, *e.g. Zygotricheae*, *Crassirameae* of the section *Conosycea* (subgenus *Urostigma*).

Associated characters of the agaonids: Absence of corbiculae to carry pollen (Fig. 10), however, some *Waterstoniella* wasps, *e.g. B. masii* and the megarhopalus group, have minute sternal corbiculae. Also, abundant male flowers with large anthers are associated with the habit of eating pollen by the females when they eclose from their galls at male phase.

Groups of agaonids which eat pollen: *Blastophaga* group A, in the subgenus *Ficus*; *Tetrapus* in the section *Pharmacosycea* of the subgenus *Pharmacosycea*; *Pleistodontes* in the section *Malvanthera* and the megarhopalus group and *Waterstoniella* in the section *Conosycea* of the subgenus *Urostigma*.

Other groups of figs usually have few male flowers per 100 galls. The male flowers (Fig. 4) are usually short-stalked (if not sessile) and have small anthers from which the pollen does not come out after dehiscence without wasp activity.

Groups of figs with few male flowers per fig: Sections *Sycidium*, *Copiosae*, and *Paleomorphe* of the subgenus *Ficus* (*sensu* Ramírez, 1974); subgenus *Sycomorus* (*sensu* Ramírez, 1974); section *Oreosycea* (subgenus *Pharmacosycea*) and sections *Americana*, *Leucogyne*, *Stilpnophyllum*, *Urostigma*, and some subseries of section *Conosycea* (subgenus *Urostigma*).

Related characters of the agaonids: They usually have conspicuous corbiculae (Fig. 11), search for ripe anthers, extract the pollen from the thecal sacs, load their corbiculae with their front legs and so far as known do not eat pollen.

Agaonids with the characters mentioned: *Agaon*, *Alfonsiella*, *Allotriozoon*, *Blastophaga* groups B, C, D, F, and G; *Ceratosolen*, *Dolichoris*, *Elisabethiella*, *Eupristina*, *Liporrhopalum*, *Maniella*, *Parapristina* and *Pegoscapus*.

THE EVOLUTION OF AGAONIDAE IN DIFFERENT GROUPS OF *FICUS*

The Agaonidae are specific not only to the species level but also to different groups of figs. Some groups of figs are inhabited by a single agaonid group (genus or subgenus). Other groups of figs have more than one agaonid genus

TABLE 2. Suggested classification of the genus *Ficus* considering the fig wasps as taxonomists; with a list of the agaonid pollinators (modified from Hill, 1967) of each group, and the presence or absence of corbiculae.

Subgenus	Section	Subsection	Agaonidae	Corbiculae		
				Absent	Sternal	Coxal
Urostigma	*Urostigma*		*Blastophaga* Group E		+	+
			Maniella		+	+
	Conosycea	*Conosycea*	*Blastophaga*		+	+?
			Megarhopalus group		+	
			Eupristina		+	+
			Waterstoniella	+		
			Waterstoniella		+	
		Dictyoneuron	*Waterstoniella*	+		
			Eupristina		+	+
		Benjamina	*Parapristina*		+	+
	Stilpnophyllum		*Blastophaga clavigera* (= *Blastophaga* Group G)		+	+?
	Malvanthera		*Pleistodontes*	+		
			Pleistodontes		+	+
	Galoclychia		*Agaon*		+	+
			Alfonsiella		+	+
			Allotriozoon		+	+
			Elisabethiella		+	+
			Paragaon		+	
	Americana		*Pegoscapus*		+	+
Pharmacosycea	*Oreosycea*		*Blastophaga* Group F		+	+
			Dolichoris		+	+
	Pharmacosycea		*Tetrapus*	+		
Ficus	*Ficus*		*Blastophaga* Group A	+		
	Rhizocladus		*Blastophaga* Group A	+		
	Kalosyce		*Blastophaga* Group A	+		
	Sinosycidium[a]					
	Eriosycea		*Blastophaga* Group B		+	
	Sycidium	*Scabrae*	*Blastophaga* Group B		+	
		Varinga	*Blastophaga* Group B		+	
	Phaeopilosae		*Blastophaga* Group C		+	
Paleomorphe	*Paleomorphe*	*Paleomorphe*	*Liporrhopalum*		+	
		Copiosae	*Blastophaga* Group D		+	

TABLE 2. (*continued*)

Subgenus	Section	Subsection	Agaonidae	Corbiculae: Absent	Corbiculae: Sternal	Corbiculae: Coxal
Sycomorus	*Adenosperma*		*Ceratosolen*		+	
	Neomorphe		*Ceratosolen*		+	
	Prostratae		*Ceratosolen*		+	
	Pungentes		*Ceratosolen*		+	
	Pseudopalmeae		*Ceratosolen*		+	
	Rivulares[b]				+	
	Sycocarpus		*Ceratosolen*		+	
	Sycomorus		*Ceratosolen*		+	

[a] Probably pollinated by a wasp of *Blastophaga*, Group A.
[b] Probably pollinated by a *Ceratosolen* wasp.

or subgenus; however, such agaonid groups are also peculiar to a single group of figs.

Table 2 shows a classification of the figs and their accompanying agaonids. Both are based on Ramírez (1974). The correspondence between groups of figs and of pollinators is evident.

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